2011. The Journal of Arachnology 39:384–392

# *Eresus kollari* (Araneae: Eresidae) calls for heathland management

**Rolf Harald Krause**[1], **Jörn Buse**[2], **Andrea Matern**[1], **Boris Schröder**[3,4], **Werner Härdtle**[1] and **Thorsten Assmann**[1]: [1]Institute of Ecology, Leuphana University Lüneburg, Scharnhorststrasse 1, 21335 Lüneburg, Germany. E-mail: Krause@uni.leuphana.de; [2]Institute of Zoology, Department of Ecology, Johannes Gutenberg-University Mainz, Johann-Joachim-Becherweg 13, 55099 Mainz, Germany; [3]Institute of Earth and Environmental Science, University of Potsdam, Karl-Liebknecht-Strasse 24-25, 14476 Potsdam, Germany; [4]Leibniz-Centre for Agricultural Landscape Research (ZALF), Eberswalder Strasse 84, 15374 Müncheberg, Germany

**Abstract.** Northwest Europe's largest heather-dominated sandy habitats are located in the nature reserve Lüneburger Heide, Germany. Yet, even these appear to be losing their ability to support some of their stenotopic species such as the ladybird spider, *Eresus kollari* Rossi 1846, and are thus becoming increasingly important for the preservation of these species. The habitat requirements of this endangered spider species were investigated in order to obtain data that will help stabilize the last remnants of the species' population in northwest Germany. Several heathland habitats were surveyed by pitfall trapping during the mate-search period of the males. Two statistical methods were applied: logistic regression and boosted regression trees (BRT). Both methods showed that three habitat variables are of prime relevance in predicting the occurrence of *E. kollari*: a) thickness of the organic layer (a negative effect), b) soil temperature at a depth of 10 cm, and c) *Calluna* cover in the herb layer (both have positive effect). Our results show that choppering (removing above-ground biomass and most of O-layer) and burning are likely appropriate heathland management measures for the conservation of *E. kollari*. Such measures improve the species' habitat quality by creating a heterogenic (small-scaled) heathland structure with suitable microhabitats. As *Calluna* heathlands show a clear senescence of the dominant heather, it is essential that those habitat patches be conserved. Further measures, such as transfer experiments, are recommended.

**Keywords:** Conservation management, habitat modeling, action plan, choppering, burning

The decline of European heathland, semi-natural habitats dominated by the heather species *Calluna vulgaris*, over the last two centuries due to changes in agricultural use and forestation (Webb 1998) has resulted in serious threats for the given habitat types, especially due to fragmentation and reduced habitat quality. Heathlands have thus been designated one of the most endangered habitat types on a European and regional scale (The Council of the European Communities 2004; Webb 1998; Keienburg et al. 2004).

Sandy heathlands do not provide a homogeneous habitat in time and space, because they are largely influenced by the developmental cycle of the dominant plant species *Calluna vulgaris* (Gimingham 1972). The largest remnants of heather-dominated sandy habitats in northwest Europe have been preserved in the Lüneburger Heide and are now part of a large nature reserve. Between 1850 and 1960, the proportion of heathland declined from 77% to 21% and today represents less than 5% of the nature reserve (Völksen 1993; Assmann 1999; Keienburg & Prüter 2004). These heathland remnants have enabled the survival of a stenotopic invertebrate fauna. However, a striking decrease in the numbers of certain stenotopic arthropod species has been observed, whereas other stenotopic heathland species still seem to be widespread (Desender et al. 1994; Assmann et al. 2003; Maes & Van Dyck 2005) or relatively stable (Gajdoš & Toft 2000).

Effective conservation of the heathland-specific arthropod species that are declining in the Lüneburger Heide can only be successful if their habitat requirements are understood and appropriate heathland management measures are implemented (Assmann & Janssen 1999). This requires detailed knowledge of the specific microhabitat in which they occur.

Assessment of distribution modeling is an important approach to obtain scientific evidence regarding the habitat preferences of selected species. Several recent studies have demonstrated the use of such models to obtain predictors for the occurrence of endangered arthropod species, including potential conservation activities (Binzenhöfer et al. 2005, 2008; Buse et al. 2007; Hein et al. 2007; Matern et al. 2007; Heisswolf et al. 2009).

Here, we report the habitat requirements of the ladybird spider *E. kollari* Rossi 1846 as an example of a stenotopic heathland species declining in number. The males' conspicuousness has made this spider a well-known species, not only among zoologists. Although its taxonomy and systematics have only recently been clarified by Řezáč et al. (2008), the decrease in numbers of *E. kollari* is well documented (Johannesen & Veith 2001). It is placed on red lists throughout Germany (Platen et al. 1996; Finch 2004).

*Eresus kollari* and its sibling species *E. sandaliatus* are both well known across northern Europe. A large-scale governmental conservation project in England involving a comprehensive action plan for *E. sandaliatus* over nearly two decades has proved successful (Hughes et al. 2009).

The aim of our research was to 1) determine the specific habitat requirements of *E. kollari* and 2) suggest specific habitat management measures aimed at conserving the last populations of the ladybird spider in northwest Germany. Bell et al. (2001) states that management based on only one species is exceptionally justifiable, and he mentions *E. cinnaberinus* (Olivier 1789; a former partial synonym of *E. kollari*) as such an exception in this sense. All in all, our study aims to preserve the last remaining populations of the ladybird spider in northwest Germany.

Figure 1.—The study area in the nature reserve Lüneburger Heide, northwest Germany. In the foreground: heather with small open patches and a pitfall trap (marked by a flag).

## METHODS

**Study species.**—*Eresus kollari* belongs to the cribellate spider family Eresidae (Platnick 2011). Male and female spiders of this species spend most of their lives underground in their well-camouflaged tube webs. The adults live in a burrow of about 1 cm diameter and a maximum depth of 10 cm. The spider weaves parts of leaves from the surrounding plants into the burrow's roof directly above the ground, making the web almost invisible throughout most of the year. It can only be found during 2 wk in May when the females strengthen the threads of the webs to catch prey for their offspring (Baumann 1997).

Males mature at the age of 2.5 yr, whereas females mature at 3–4 yr (Baumann 1997). Only males leave the burrow to mate at the end of their lives for a period of ~ 2 wk between August and October. In their nuptial dress, they search for females within a diameter of ~ 10–12 m. Males and females share precisely the same habitat, and both show a very low dispersal potential (Baumann 1997).

**Study area.**—The study area (Fig. 1) is situated in the nature reserve Lüneburger Heide about 6 km east of Schneverdingen (53°7′43N, 09°52′45E). The nature reserve includes the most extensive heathlands of northwest Germany, covering an area of ~ 5,000 ha. Niemeyer et al. (2007) characterize the climate of the nature reserve as a humid suboceanic type with a mean annual precipitation of 811 mm and a mean annual temperature of 8.4° C. They describe the soil as Pleistocene sandy deposits and nutrient-poor podzols or podzolic soils, pH range 3.2–3.6. Old, high heather shrubs covered the whole study site at least from the 1960s to the 1980s (Lütkepohl 1993). Since 2002, the last year in which the heather was mown, management practices have halted (Mertens pers. comm.).

Our study was carried out in 2007. The study area was subdivided into three parts in which we placed 100 pitfall traps. Part A (100 by 130 m, 60 traps) appeared fairly homogenous and consisted mainly of young, low heather plants with open patches, lichens, and moss. Part B (140 by 200 m, 30 traps), directly adjoining Part A, consisted of older heather, mainly 50–100 cm height, and interspersed with birch trees. Part C (10 traps, 5 in the forest and 5 in the grassland area), 400 m distant from part B, was an area of coniferous forest and forest edge with high grass scattered with young trees. All pitfalls were placed in rows, each holding 10 traps.

**Sampling and predictor variables.**—We applied a stratified random sampling approach to sample species occurrence and environmental data (cf. Hirzel & Guisan 2002). Direct observation of individuals or webs would be the best method to record species occurrence in the field. However, as the webs are difficult to find, we used pitfall trapping instead.

As female and male spiders share exactly the same habitat and stay in their webs during their whole life spans, our data can be applied to both sexes, although our information is only based on capture of males. They only leave their burrows at the end of their lives to search for females in close vicinity of their burrows (Bellmann 1997; Baumann 1997).

From 14 August 2007 to 16 October 2007, during the mate-searching period of the males, we used 100 pitfall traps. Plastic, 10 cm diam. cups were used, covered with a piece of netting wire to prevent larger animals from falling in. The

traps were filled with a mixture of 50% ethanol, 20% glycerine, and 30% water (modified after Renner 1982) as a preservative. The traps were emptied fortnightly. Nineteen environmental variables were recorded from each trap loeation. Habitat structure strongly influences the occurrence of spider species (cf. Schwab et al. 2002; Ziesche & Roth, 2008), so we thus selected and analyzed the variables that describe the habitat in terms of temperature, moisture, and structure. The vegetation cover of the dominant vascular plant species in different vegetation layers was estimated within a diameter of 1 m around each trap.

We analyzed vegetation cover in 3 different layers a) 0–10 cm, b) 10–50 cm, c) > 50 cm, estimating the percentage cover of the main vegetation components like *Calluna vulgaris* and/or *Erica tetralix* as well as grasses, lichens, bare soil, moss, and trees. Additionally, we measured the thickness of the organic layer (cm). We also collected the data of the temperature of the top soil and the soil at 10 cm depth (° C). Insolation (Lux) and temperature (° C) data were taken separately on 5 September, a sunny day, over midday by means of a photometer and a digital thermometer with a 10-cm-long metal rod. We took a spadeful of soil sample of every trap to measure the pH-value ($pH_{H2O}$), organic matter content (%), and water content (%) of the A-horizon.

**Statistical analysis.**—To estimate the occurrence probabilities of *E. kollari* depending on environmental predictor variables, we used two different approaches: logistic regression as a standard parametric approach and boosted regression trees (BRT), a promising, non-parametric ensemble forecasting technique (cf. Elith et al. 2008). To achieve the best balanced predictive model, we used $P_{fair}$ as the appropriate classification threshold (according to Schröder & Richter 1999). The threshold $P_{fair}$ ensures that sensitivity (= percentage of correctly predicted presences) and specificity (= percentage of correctly predicted absences) of the model have the same magnitude.

For our logistic regression analysis, we first performed univariate logistic regressions for each of the predictor variables, following the approach of Hosmer & Lemeshow (2000). Only predictors with $P < 0.25$ in the univariate logistic regression were considered as potential candidates for multiple regression analysis. Significance in the logistic regression model was assessed using the likelihood ratio test. To assess correlation between predictors, we analyzed their bivariate correlation structure. None of the potential candidates showed a bivariate correlation stronger than $r_s = 0.553$ (Spearman rank-correlation test). Within the multiple regression model, we also tested the significance of two-way interaction terms and quadratic terms for each of the previously selected predictors. None of the interaction terms and only one of the quadratic terms (moss layer in herbage cover) was significant ($P < 0.05$), but this is not considered in the final model. From the resulting set of predictors, we deleted those with a significance level of $P > 0.1$ from this model. In a further step, backwards stepwise selection ('fastbw': Harrell 2001) was used to prove the importance of the predictors left in the final model. This method uses the fitted complete model and computes approximate Wald statistics by computing conditional (restricted) maximum likelihood estimates, assuming multivariate normality of estimates.

Nagelkerke's $R^2$ was used for evaluating model calibration. To assess model discrimination and performance, we used the program ROC_AUC provided by Schröder (2006) to calculate the AUC (area under a receiver operating characteristic curve: Swets 1988) and some threshold-dependent criteria such as the correct classification rate and Cohen's kappa. To quantify the total independent contribution of the single predictors considered in the logistic regression, we ran a hierarchical partitioning procedure (MacNally 2000; Heikkinen et al. 2005; Müller et al. 2009; Schröder et al. 2009).

Habitat models run the risk of being overfitted to the training data (Harrell 2001; Steyerberg et al. 2001; von dem Bussche et al. 2008). As independent data were not available to correct for this optimism, we used bootstrapping with 100 replicates to correct the measures of model performance (e.g., Peppler-Lisbach & Schröder 2004; Oppel et al. 2004). This method allows almost unbiased estimates of model performance and was found to provide the best estimate of internal validity of predictive logistic regression models (Reineking and Schröder 2003; Schröder 2008).

To compare these results with a more flexible non-parametric approach, we also built boosted regression trees (BRT, see Elith et al. 2008 for details). This approach combines the boosting algorithm (Schapire & Singer 1999) with classification and regression trees (De'ath & Fabricius 2000), leading to a set of several hundreds or thousands of trees in the final model (De'ath 2007). It has the advantage that it allows for an implicit modeling of thresholds as well as interactions between predictors. BRTs were estimated with a tree complexity of 5 and a learning rate of 0.001. Variable selection was performed in a forward stepwise manner, so that only important predictors are considered in the final model. The approach makes it possible to calculate the contributions of all predictors in explaining the variability of the response variable. Model performance in terms of AUC and Nagekerke's $R^2_N$ was evaluated based on tenfold cross-validation. For both methods, residuals were checked for spatial autocorrelation by calculating global Moran's I (Dormann et al. 2007) and spline correlograms (Bjørnstad & Falck 2001; Schröder 2008).

We carried out the statistical analyses with R 2.7.1 (R Development Core Team 2008). Hierarchical partitioning was conducted using the 'hier.part'-library (version 1.0, MacNally & Walsh 2004), and the 'Hmisc' (version 3.0-12) and 'Design' library (version 2.0-12) (Harrell 2001) were used for the logistic regression procedure. The library 'gbm' (provided by G. Ridgeway, supported by some functions provided by J. Elith and J. Leathwick) was used for boosted regression tree modeling. Response curves of logistic regressions were plotted using the program LR-mesh provided by Rudner (2004). Spatial autocorrelation was checked by applying the library 'spdep' (Bivand 2006).

## RESULTS

In total, 95 *E. kollari* specimens, all of which were males, were found in 48 of the 100 pitfalls. In 26 traps, we found only one individual of the studied species, with a maximum of six found in two of the traps. In part A of the study site, spiders fell into 41 of 60 traps. We observed positive spatial autocorrelation in the raw presence-absence data within a

Table 1.—Parameter estimates of the multiple logistic regression model explaining the occurrence of *E. kollari* (residual deviance = 104.90 on 96 degrees of freedom, null devianee = 138.47 on 99 degrees of freedom). Significance values for each coefficient were obtained from Wald tests. Although not significant at $\alpha = 0.05$, $\beta_3$ was left in the model because of its contribution to the model evaluated with Wald statistics in the stepwise backwards selection of variables.

| Variable | Regression coefficient | *SE* | Wald Z | *P* |
|---|---|---|---|---|
| $\beta_1$ Soil temperature at 10 cm depth | 0.591 | 0.226 | 2.61 | 0.009 |
| $\beta_2$ Thickness of organic layer | −0.360 | 0.159 | −2.27 | 0.023 |
| $\beta_3$ *CallunalErica* cover in herb layer | 0.015 | 0.009 | 1.71 | 0.087 |
| $\beta_0$ Intercept | −8.420 | 3.556 | −2.37 | 0.018 |

50 m distance from each trap (partial Moran's I statistic standard deviate = 9.119, $P < 0.001$).

**Habitat variables related to species presence.**—The final logistic regression model considers three predictors with a strong effect on occurrence probability (Table 1). 'Thickness of organic layer' ($R^2_N = 0.28$ in a univariate regression, $P < 0.001$) had a negative effect on the occurrence probability of *E. kollari*. In contrast, 'soil temperature at 10 cm depth' ($R^2_N = 0.22$, $P < 0.001$), and '*Calluna* cover in herb layer' ($R^2_N = 0.15$, $P < 0.01$) both had a positive effect (Fig. 2). At our study site, these variables covered a large gradient, range of 12.4–17.3° C in soil temperature and range of 0–12 cm in the thickness of the organic layer, whereas the height of *Calluna* reached 8–50 cm and its soil coverage was 3–100%. Occurrence probabilities of 50% are explained by a minimum soil temperature of 15° C and a maximum organic layer of 3 cm (Figs. 2, 3).

The final logistic regression model explained a considerable proportion of the overall variance in our dataset ($R^2_N = 0.38$). A first model containing predictors that were associated with the outcome of the final model ($P < 0.25$, according to Hosmer & Lemeshow 2000) explained slightly more variance in our dataset ($R^2_N = 0.44$), but some predictors were removed ('heather in herb layer,' the cover of 'herbage in moss and herb layer,' 'soil temperature on surface,' 'intensity of light on surface') in the stepwise model selection process for the final model.

In order to quantify the independent contribution of the predictor variables considered in both the logistic regression and the BRT model, we conducted a hierarchical partitioning analysis. The results for the logistic regression model show the relatively high influence of the organic layer (44.0%). The independent effect of soil temperature at 10 cm depth was also quite high (35.5%), whereas the cover of heather in the herb layer had an independent effect of 20.5%.

Soil temperature at 10 cm depth (27.6%) and thickness of the organic layer (22.6%) best explained the variability of the response variable in the BRT model. Other variables such as soil water content, insolation, heather cover in the herb layer, and proportion of organic matter in the soil contributed

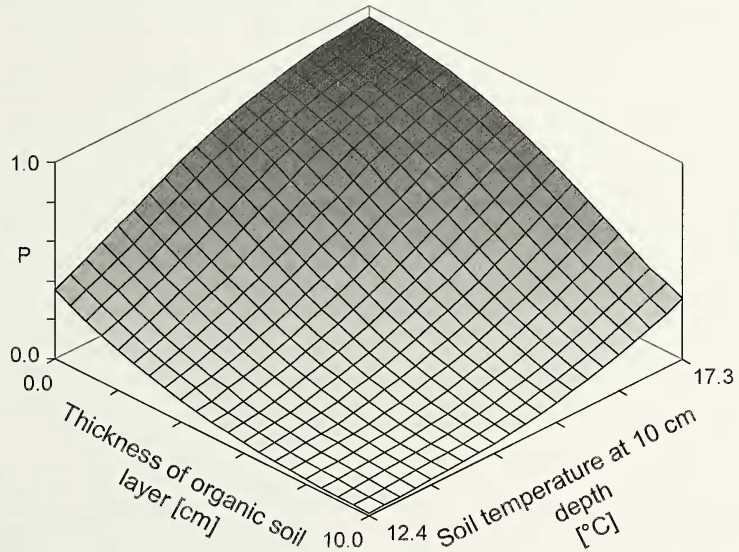


Figure 2.—Bivariate response surface of the two most important predictors in the final logistic regression model (see Table). The estimated occurrence probability (P) of *E. kollari* is plotted against the two continuous predictors.

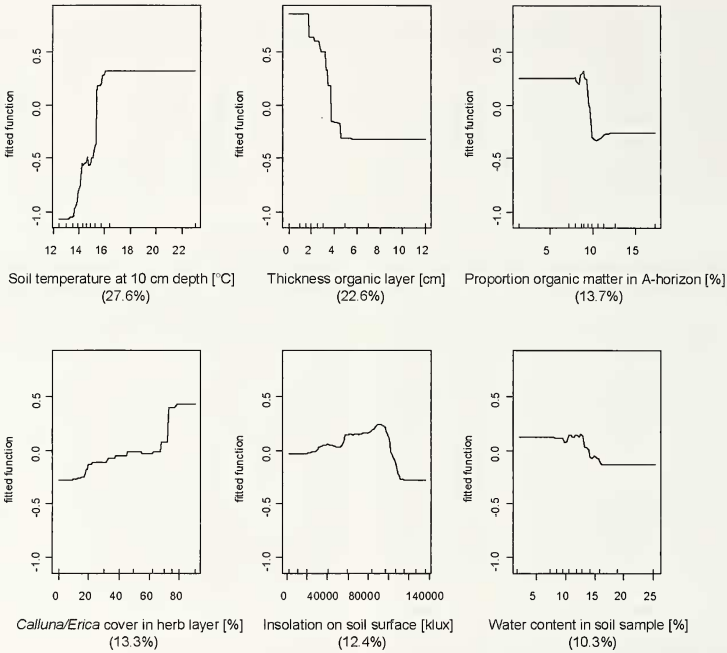


Figure 3.—Univariate response curves of the six most influential variables derived from the BRT model: Soil temperature at 10 cm depth; thickness of organic layer; proportion of organic matter in A-horizon; *Calluna/Erica* cover in herb layer; insolation on soil surface; water content in soil sample. The relative influence of each variable in the model is given in parentheses.

between 10.3 and 13.7% to the variability in the response variable (Fig. 3).

**Model performance and validation.**—The logistic regression model showed a relatively good discriminative power with an AUC-value of 0.80 ($CI_{95\%}$: 0.72–0.89). Using $P_{fair}$ in the model, we reached a correct classification rate of 75%. The evaluation of Cohen's kappa indicates good predictive power for our final model. Internal validation by bootstrapping revealed only slight overfitting of the final model. Corrected values were $R^2_N$ = 0.34 and AUC-value = 0.78, which indicates acceptable discriminative performance. This shows that our model is robust within the study site.

Accordingly, the BRT model reached an AUC = 0.80 and $R^2_N$ = 0.253 after tenfold cross-validation and an apparent model performance of AUC = 0.91 ($CI_{95\%}$: 0.85–0.96) and $R^2_N$ = 0.53, CCR = 0.81 and kappa = 0.62. Neither the logistic regression (Moran's I statistic standard deviate = 0.068, $P$ = 0.473) nor the BRT approach (Moran's I statistic standard deviate = 0.929, $P$ = 0.176) showed any residual spatial autocorrelation.

## DISCUSSION

Our study describes the ecological demands of this spider species in the last remaining heathland areas in Germany. Our logistic regression model indicates that the occurrence of *E. kollari* in the large heathland complex of northwest Germany is influenced primarily by the three habitat variables. Here we discuss the effect of each variable.

1) There was a negative effect of the thickness of the organic layer. The layer functions as an obstacle to the male's locomotory behavior in the sense of spatial resistance (Duffey 1962). This means that the management measures should strive to maintain a rather thin organic layer of maximum 3 to 4 cm. This is of great importance not only for males, since both sexes have to penetrate the organic layer in order to dig their burrows (Baumann 1997).

2) The models showed a positive effect of temperature at 10 cm depth, but not at the surface. This is likely due to the fact that the males, like the females, spend nearly all their lives in burrows dug in soil. This variable may affect the occurrence of females rather than males, since females prefer higher temperature places for quick development of brood (cf. Klein et al. 2005).

The soil surface temperature fluctuated from trap to trap. This variable was excluded by the automatic model selection procedure for the logistic regression model, but had an explanatory power of 12.4% in the boosted regression trees (Fig. 3). Hence, the occurrence of the males during the vagrant period (Baumann 1997) is less influenced by the surface temperature than by the soil temperature deeper in the ground.

3) Both models demonstrated that '*Calluna* cover in the herb layer' also has a fairly strong influence (with 13.3% in the BRT-model) on the occurrence of the species. However, our models cannot distinguish between the influence of *Calluna* cover in the herb layer and the importance of the moss layer. Other authors have pointed out that *Eresus* prefers wind-protected sites (Wiehle 1953; Bellmann 1997; Baumann 1997). This may explain why *E. kollari* prefers sites in which heather is higher than 10 cm but lower than 50 cm, since this vegetation height allows enough wind-shelter, but also provides sufficient insolation to reach the required temperature at a depth of 10 cm. Hence, *E. kollari* can be considered as a stenotopic thermophilic species of dry heathlands.

Our statistical models revealed habitat variables that can be used to predict the occurrence of *E. kollari* with a correct classification rate ranging from 75 up to 83% and with considerable discriminative power. Since we built a predictive distribution model based on presence and absence data from trapping in the field, the circumstances under which AUC could be a misleading performance measure do not apply to our study (Lobo et al. 2008). Higher AUC scores can likely be obtained by increasing the geographical extent of models (Lobo et al. 2008) because of the larger environmental distances of the absences. Nevertheless, the results of the distribution model presented here are limited to the predictors used and, to some extent, to the location from which the data were obtained. Internal validation revealed only slight overfitting, but further analysis is necessary to determine whether the model is generally applicable to other regions. In general, both the BRT and the logistic regression model seem to be robust (bootstrapping) within the investigated study site.

As *E. kollari* was not found in 19 of the 60 pitfall traps in the most suitable part of our study site (part A), we assume that it could follow the metapopulation dynamics reported from other arthropod stenotopic heathland species (Habel et al. 2007; Assmann & Janssen 1999; Drees et al. 2011). This may also be the reason why our statistical models do not explain more than 38% of the occurrence of *E. kollari* on our study site.

The dispersal power of *E. kollari* is too low to colonize or recolonize empty habitat patches, at least under the conditions of the highly fragmented heathland patches in the nature reserve Lüneburger Heide (cf. Eggers et al. 2010). Baumann (1997) proved low dispersal power by marking 1,004 individuals of *Eresus*. Recaptures showed that this species has a very poor dispersal potential, since the offspring build their new burrows in close proximity to their mother's web. Baumann's studies on males have shown that spatial resistance is of great importance to these animals; thus, males do not move farther than 10 to 12 m on average from their own burrows. The farthest distance moved by a single spider was 61 m.

Therefore, both low dispersal power and the spatially structured populations, as indicated by positive spatial autocorrelation within the first 50 m around occurrences, should result in a decline of the species if heathland areas are strongly fragmented. This decline has already been recognized (Platen et al. 1998; Blick et al., in press). Proof of the existence of non-occupied, though suitable patches for an *Eresus* species has already been given by a successful transfer experiment in England with *E. sandaliatus*, a sibling species of *E. kollari* (Hughes et al. 2009). This result can be best explained by a metapopulation structure in *E. sandaliatus*.

**Conclusions for a sound conservation strategy.**—Due to both the spatially structured populations and the probable existence of unoccupied habitat patches, we recommend re-introduction experiments with *E. kollari* to habitat patches that seem to belong to the same type of patches. Monitoring of the re-introduction effort is also strongly recommended.

Three main variables (thickness of the organic layer, soil temperature at 10 cm depth, *Calluna* cover in the herb layer) have been shown to be decisive for the occurrence of the ladybird spider. Based on these variables, we recommend the implementation of an elaborated management plan that guarantees long-term heathland quality (cf. McFerran et al. 1995; Bell et al. 2001) and can accommodate the habitat requirements of *E. kollari*:

1) Choppering is a management measure that creates bare soil by removing the above-ground biomass and most parts of the O-layer, with only a thin layer of organic material remaining on the surface (Niemeyer et al. 2007). It promotes the heterogeneity of heathland soil by removing the small ridges and maintaining the micro-relief. Thus, after being choppered, the raw-humus layer would offer a huge variety of suitable combinations of the variables 'organic layer' and '*Calluna* coverage' suggested by our habitat model. In part A of our study area, the last heathland management measure, 'mulch mowing,' took place in 2002. Mowing, too, seems to be an appropriate measure for conservation of the *E. kollari* population and probably also for other European *Eresus* species on different sites (Usher 1992; Bell et al. 2001).

2) We also recommend prescribed burning, since it leaves the temperatures unchanged at a depth of a few centimeters so that it cannot harm the spider in its tube webs; the whole process also leaves the micro-relief untouched (McFerran et al. 1995; Niemeyer et al. 2005). The structure after burning might also provide appropriate habitat. However, the raw humus layer required by E. *kollari* will only be restored after several years. Grasses (e.g., *Molinia careulea*) regenerate after prescribed burning, but break down only after the second year (Niemeyer et al. 2005; Härdtle et al. 2009).

Usher (1992) suggests that the habitats of such a rare species as *Eresus kollari* should be managed throughout Europe. As a basic principle, if management measures are not applied in heathlands, it will not be possible to ensure the long-term preservation of this habitat (Usher 1992; Härdtle et al. 2007). For choppering, we recommend that a pattern of strips or a fishbone-structure should be employed in *E. kollari* conservation measures, so that the spiders have the chance to move from the untouched colonized habitat patches into the managed areas in order to colonize or recolonize empty habitat patches. The measures should be applied at a distance of a maximum of 50 m as well. We would recommend that the strips should be not broader than the machine used, and the patches chosen for choppering should be narrow enough to allow the spider to move over. It is also very important to leave some time (ca 5 yr) after the measures have been carried out for the development or redevelopment of these sites, and to spread the measures cyclically and periodically in space and time.

Our knowledge of the effects of management measures on arthropod fauna is still poor, and long-term studies are only available for ground beetles in the Netherlands (den Boer & van Dijk 1995). These studies report that some endangered species, typical for heathlands, benefit from burning and choppering (or, in some cases, sod cutting). The only known long-term study of the dynamics of heathland spider species does not refer to the effects of habitat management (Gajdoš & Toft 2000). Only long-term monitoring (over at least 10 years) will be able to show what impact the management measures recommended as a result of our habitat suitability model will have on the endangered spider species *E. kollari.*

## ACKNOWLEDGMENTS

We are grateful to the Verein Naturschutzpark e.V., especially to Dirk Mertens, for assisting us with his expert knowledge in the field, and to the Alfred Toepfer Academy (NNA) for permission to collect the samples in the nature reserve. Furthermore, we thank Dr. Thomas Niemeyer, Leuphana University Lueneburg, for fruitful discussions and hints regarding heathland ecology and measures.

## LITERATURE CITED

Assmann, T. 1999. The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). Biodiversity and Conservation 8:1499–1517.

Assmann, T. & J. Janssen. 1999. The effects of habitat changes on the endangered ground beetle *Carabus nitens* (Coleoptera: Carabidae). Journal of Insect Conservation 3:107–116.

Assmann, T., W. Dormann, H. Främbs, S. Gürlich, K. Handke, T. Huk, P. Sprick & H. Terlutter. 2003. Rote Liste der in Niedersachsen und Bremen gefährdeten Sandlaufkäfer und Laufkäfer mit Gesamtverzeichnis. Informationsdienst Naturschutz Niedersachsen 23(2):70–95.

Baumann, T. 1997. Populationsökologische und zönotische Untersuchungen von Habitatqualität und Habitatfragmentierung für Spinnenpopulationen auf Trockenrasen am Beispiel von *Eresus cinnaberinus* (Oliv. 1789). Dissertation, University of Bremen. Wissenschaft und Technik Verlag, Berlin.

Bell, J.R., C.P. Wheater & W.R. Cullen. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of Zoology 255:377–387.

Bellmann, H. 1997. Kosmos Atlas Spinnentiere Europas. Kosmos, Stuttgart.

Binzenhöfer, B., B. Schröder, R. Biedermann, B. Strauss & J. Settele. 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*. Biological Conservation 126:247–259.

Binzenhöfer, B., R. Biedermann, J. Settele & B. Schröder. 2008. Connectivity compensates for low habitat quality and small patch size in the butterfly *Cupido minimus*. Ecological Research 23:259–269.

Bivand, R. 2006. Implementing spatial data analysis software tools. R. Geography Analysis 38:23–40.

Bjørnstad, O.N. & W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics 8:53–70.

Blick, T., P. Bliss, R. Drogla, O. Finch, M. Gerisch, A. Haenggi, K.H. Harms, J. Kiechle, C. Komposch, A. Malten, D. Martin, C. Muster, D. Nährig, R. Platen, I. Roedel, P. Sacher, M. Scheidler, A. Schoenhofer, A. Staudt, H. Stumpf & D. Tolke. In press. Rote Liste der Spinnen Deutschlands (Arachnida: Araneae). Status March 2008.

Buse, J., B. Schröder & T. Assmann. 2007. Modelling habitat and spatial distribution of an endangered longhorn beetle - A case study for saproxylic insect conservation. Biological Conservation 137:372–381.

Desender, K., M. Dufrêne & J.P. Maelfait. 1994. Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century. Pp. 247–252. *In* Carabid Beetles - Ecology and Evolution. (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff & J.P. Maelfait, eds.). Kluwer, Dordrecht.

De'ath, G. & K.E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

Den Boer, P.J. & T.S. van Dijk. 1995. Carabid beetles in a changing environment. Wageningen Agricultural University Papers 94:1–30.

Dormann, C.F., J.M. McPherson, M.B. Araújo, R. Bivand, J. Bolliger, G. Carl, R. Davis, A. Hirzel, W. Jetz, W.D. Kissling, I. Kühn, R. Ohlemüller, P.R. Peres-Neto, B. Reineking, B. Schröder, F.M. Schurr & R. Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data. Ecography 30:609–628.

Drees, C., H. de Vries, W. Härdtle, A. Matern, M. Persigehl & T. Assmann. 2011. Genetic erosion in a stenotopic heathland ground beetle (Coleoptera: Carabidae): a matter of habitat size? Conservation Genetics 12:105–117.

Duffey, E. 1962. A population study of spiders in limestone grassland. Journal of Animal Ecology 31:571–599.

Eggers, B., A. Matern, C. Dress, J. Eggers, W. Härdtle & T. Assmann. 2010. Value of semi-open corridors for simultaneously connecting open wooded habitats: a case study with ground beetles. Conservation Biology 24:256–266.

Elith, J., J.R. Leathwick & T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Finch, O.D. 2004. Rote Liste der in Niedersachsen und Bremen gefährdeten Webspinnen (Araneae). Informationsdienst Naturschutz Niedersachsen 24(5):1–20.

Gajdoš, P. & S. Toft. 2000. A twenty-year comparison of epigeic spider communities (Araneae) of Danish coastal heath habitats. Journal of Arachnology 28:90–96.

Gimingham, C.H. 1972. Ecology of Heathlands. Chapman & Hall, London.

Habel, J.C., T. Schmitt, W. Härdtle, M. Lütkepohl & T. Assmann. 2007. Dynamics in a butterfly-plant-ant system: influence of habitat characteristics on turnover rates of the endangered lycaenid *Maculinea alcon*. Ecological Entomology 32:536–543.

Härdtle, W., T. Niemeyer, T. Assmann, H. Meyer & G. von Oheimb. 2007. Can prescribed burning compensate for atmospheric nutrient loads in wet heathlands? Phytocoenologia 37:161–174.

Härdtle, W., O. von Oheimb, A.-K. Gerke, M. Niemeyer, T. Niemeyer, T. Assmann, C. Drees, A. Matern & H. Meyer. 2009. Shifts in N and P budgets of heathland ecosystems: effects of management and atmospheric inputs. Ecosystems 12:298–310.

Harrell, F.E. 2001. Regression Modeling Strategies. Springer, New York.

Heikkinen, R.K., M. Luoto, M. Kuussaari & J. Pöyry. 2005. New insights into butterfly–environment relationships using partitioning methods. Proceedings of the Royal Society - Biological Science B 272:2203–2210.

Hein, S., J. Voss, H.-J. Poethke & B. Schröder. 2007. Habitat suitability models for the conservation of thermophilic grasshoppers and bush crickets. Journal of Insect Conservation 11:221–240.

Heisswolf, A., S. Reichmann, H.-J. Poethke, B. Schröder & E. Obermaier. 2009. Habitat quality matters for the distribution of an

endangered leaf beetle and its egg parasitoid in a fragmented landscape. Journal of Insect Conservation 13:165–175.

Hirzel, A. & A. Giusan. 2002. Which is the optimal strategy for habitat suitability modelling? Ecological Modelling 157:331–341.

Hosmer, D.W. & S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York.

Hughes, I., R. Key, P. Merrett, A. Nicholson & D. Heaver. 2009. The Ladybird Spider in Britain – its history, ecology and conservation. British Wildlife 20:153–159.

Johannesen, J. & M. Veith. 2001. Population history of *Eresus cinnaberinus* (Araneae: Eresidae) colour variants at a putative species transition. Heredity 87:114–124.

Keienburg, T., J. Prüter, W. Härdtle, T. Kaiser, A. Koopmann, A. Melber, F. Niemeyer & S. Schaltegger. 2004. Feuer und Beweidung als Instrumente zur Erhaltung magerer Offenlandschaften in Nordwestdeutschland. NNA-Berichte 17(2):3–12.

Keienburg, T. & J. Prüter. 2004. Conservation and Management of Central European Lowland Heathlands. Case Study: Lüneburger Heide Nature Reserve, North-West Germany. Heathguard, The Heathland Centre, Lygra, Norway.

Klein, B.A., T.C. Bukowski & L. Avilés. 2005. Male residency and mating patterns in a subsocial spider. Journal of Arachnology 33:703–710.

Kuhk, R. & W. Rabeler. 1956. *Eresus niger* (Pet.), Araneina, auf norddeutschen Zwergstrauchheiden. Steiniger, Natur und Jagd in Niedersachsen, Hannover, 211–214.

Lobo, J.M., A. Jimenez-Valverde & R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17:145–151.

Lütkepohl, M. 1993. Schutz und Erhaltung der Heide. Leitbilder und Methoden der Heidepflege im Wandel des 20. Jahrhunderts am Beispiel des Naturschutzgebietes Lüneburger Heide. NNA-Berichte 6(3):10–20.

MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodiversity and Conservation 9:655–671.

MacNally, R. & C.J. Walsh. 2004. Hierarchical partitioning public-domain software. Biodiversity and Conservation 13:659–660.

Maes, D. & H. Van Dyck. 2005. Habitat quality and biodiversity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. Biological Conservation 123:177–187.

McFerran, D.M., J.H. McAdam & W.I. Montgomery. 1995. The impact of burning and grazing of heathland plants and invertebrates in country Antrim. Biology and Environmental-Proceedings of the Royal Irish Academy 95B:1–17.

Matern, A., C. Drees & M. Kleinwächter. 2007. Habitat modelling for the conservation of the rare ground beetle species *Carabus variolosus* (Cololeoptera, Carabidae) in the riparian zones of headwaters. Biological Conservation 136:618–627.

Müller, J., J. Pöllath, R. Moshammer & B. Schröder. 2009. Predicting the occurrence of middle spotted woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data. Forest Ecology Management 257:502–509.

Niemeyer, M., T. Niemeyer, S. Fottner, W. Härdtle & A. Mohamed. 2007. Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. Biological Conservation 134:344–353.

Niemeyer, T., M. Niemeyer, A. Mohamed, S. Fottner & W. Härdtle. 2005. Impact of prescribed burning on the nutrient balance of heathlands with particular reference to nitrogen and phosphorus. Applied Vegetation Science 8:183–192.

Oppel, S., H.M. Schaefer, V. Schmidt & B. Schröder. 2004. Habitat selection by the pale-headed brush-finch, *Atlapetes pallidiceps*, in southern Ecuador: implications for conservation. Biological Conservation 118:33–40.

Platen, R., T. Blick, P. Sacher & A. Malten. 1996. Rote Liste der Webspinnen Deutschlands (Arachnida: Araneae). Arachnologische Mitteilungen 11:5–31.

Peppler-Lisbach, C. & B. Schröder. 2004. Predicting the species composition of mat-grass communities (Nardetalia) by logistic regression modelling. Journal of Vegetation Science 15:623–634.

Platnick, N.I. 2011. The World Spider Catalog, Version 11.5. The American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog/INTRO1.html.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at http://www.R-project.org.

Reineking, B. & B. Schröder. 2003. Computer-intensive methods in the analysis of species-habitat relationships. Pp. 165–182. *In* Gene Bits und Ökosysteme - Implikationen neuer Technologien für die ökologische Theorie. (H. Reuter, B. Breckling & A. Mitwollen, eds.), Theorie in der Ökologie, Volume 9. Peter Lang, Frankfurt am Main.

Renner, K. 1982. Coleopterenfänge mit Bodenfallen am Sandstrand der Ostseeküste, ein Beitrag zum Problem der Lockwirkung von Konservierungsmitteln. Faunistisch-ökologische Mitteilungen 5:137–146.

Řezáč, M., S. Pekár & J. Johannesen. 2008. Taxonomic review and phylogenetic analysis of central European *Eresus* spiders (Araneae: Eresidae). Zoologica Scripta 37:263–287.

Rudner, M. 2004. LR-Mesh - Response surfaces for logistic regression models. Computer program, version 1.0.5. Online at http://www.uni-oldenburg.de/landeco/21343.html

Schapire, R.E. & Y. Singer. 1999. Improved boosting algorithms using confidence-rated predictions. Mach Learn 37:297–336.

Schröder, B. & O. Richter. 1999. Are habitat models transferable in space and time? Zeitschrift fur Ökologie und Naturschutz 8:195–205.

Schröder, B. 2006. ROC & AUC-Calculation – evaluating the predictive performance of habitat models. Online at http://brandenburg.geoecology.uni-potsdam.de/users/schroeder/download.html

Schröder, B. 2008. Challenges of species distribution modeling below ground. Journal of Plant Nutrition and Soil Seience 171:325–337.

Schröder, B., B. Strauss, R. Biedermann, B. Binzenhöfer & J. Settele. 2009. Predictive species distribution modeling in butterflies. *In* Ecology of Butterflies in Europe. (J. Settele, T.G. Shreeve, M. Konvicka & H. van Dyck, eds.). Cambridge University Press, Cambridge, UK.

Schwab, A., D. Dubois, P.M. Fried & P.J. Edwards. 2002. Estimating the biodiversity of hay meadows in north-eastern Switzerland on the basis of vegetation structure. Agriculture Ecosystems & Environment 93:197–209.

Steyerberg, E.W., M. Eijkemans & J. Habbema. 2001. Application of shrinkage techniques in logistic regression analysis: a case study. Statistica Neerlandica 55:76–88.

Swets, J.A. 1988. Measuring the accuracy of diagnosis systems. Science 240:1285–1293.

The Council of the European Communities. 2004. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora - Consolidated Text. Office for Official Publications of the European Communities.

Usher, M.B. 1992. Management and diversity of arthropods in *Calluna* heathland. Biodiversity and Conservation 1:63–79.

Völksen, G. 1993. Die Entstehung der Kulturlandschaft, Lüneburger Heide". NNA-Berichte 6(3):4–10.

von dem Bussche, J., R. Spaar, H. Schmid & B. Schröder. 2008. Modelling the recent and potential future spatial distribution of ring ouzel (*Turdus torquatus*) and blackbird (*T. merula*) in Switzerland. Journal of Ornithology 149:529–544.

Webb, N.R. 1998. The traditional management of European heathlands. Journal of Applied Ecology 35:987–990.

Wiehle, H. 1953. Spinnentiere oder Arachnoidea (Araneae) IX: Orthognatha – Cribellatae – Haplogynae – Entelegynae. Pp. 70–75. *In* Die Tierwelt Deutschlands, 42. Teil. (F. Dahl, ed.). VEB Gustav Fischer, Jena.

Ziesche, M. & M. Roth. 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat? Forest Ecology and Management 255:738–752.

*Manuscript received 15 September 2010, revised 11 March 2011.*